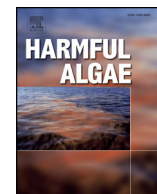




Contents lists available at ScienceDirect

Harmful Algae

journal homepage: www.elsevier.com/locate/hal

Perspective: Advancing the research agenda for improving understanding of cyanobacteria in a future of global change

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ARTICLE INFO

Keywords:

Climate change

cyanoHABs

Temperature

CO₂

ABSTRACT

Harmful cyanobacterial blooms (=cyanoHABs) are an increasing feature of many waterbodies throughout the world. Many bloom-forming species produce toxins, making them of particular concern for drinking water supplies, recreation and fisheries in waterbodies along the freshwater to marine continuum. Global changes resulting from human impacts, such as climate change, over-enrichment and hydrological alterations of waterways, are major drivers of cyanoHAB proliferation and persistence. This review advocates that to better predict and manage cyanoHABs in a changing world, researchers need to leverage studies undertaken to date, but adopt a more complex and definitive suite of experiments, observations, and models which can effectively capture the temporal scales of processes driven by eutrophication and a changing climate. Better integration of laboratory culture and field experiments, as well as whole system and multiple-system studies are needed to improve confidence in models predicting impacts of climate change and anthropogenic over-enrichment and hydrological modifications. Recent studies examining adaptation of species and strains to long-term perturbations, e.g. temperature and carbon dioxide (CO₂) levels, as well as incorporating multi-species and multi-stressor approaches emphasize the limitations of approaches focused on single stressors and individual species. There are also emerging species of concern, such as toxic benthic cyanobacteria, for which the effects of global change are less well understood, and require more detailed study. This review provides approaches and examples of studies tackling the challenging issue of understanding how global changes will affect cyanoHABs, and identifies critical information needs for effective prediction and management.

1. Introduction

Cyanobacteria originated more than 2.5 billion years ago, evolved through periods of dramatic oxygen increases, CO₂ declines and climatic variations during the Earth's history, and diversified into a wide range of natural habitats. At present, cyanobacteria play a key role in the global carbon and nitrogen cycles, as well as being an important component in many aquatic food webs. In bloom proportions, however, they can have major environmental, social and economic impacts (O'Neil et al., 2012; Huisman et al., 2018). This includes causing hypoxic conditions, resulting in fish kills and changes in the nutrient biogeochemistry of a waterbody, as well as affecting the diversity and abundance of other species. The economic costs of harmful

cyanobacterial blooms (thereafter cyanoHABs) can be massive. For example, in the United States the costs have been estimated to be US \$2.2 billion p.a., via the effects on water quality, recreation use, fishing and property values (Dodds et al., 2008). Toxic cyanoHABs in Lake Taihu (China) and Lake Erie (USA) have led to major drinking water crises in large cities (Guo, 2007; Qin et al., 2010; Bullerjahn et al., 2016), and the removal of cyanobacteria and their toxins from drinking water reservoirs may lead to high water treatment costs (see review by Hamilton et al., 2014a). Globally, these economic costs are predicted to increase over time due to increasing incidences of cyanoHABs from continued eutrophication and a warming climate (Wagner and Adrian, 2009; Carey et al., 2012; Visser et al., 2016).

Predicting the magnitude, intensity and duration of cyanoHABs, and

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<https://doi.org/10.1016/j.hal.2019.04.004>

Received 4 April 2019; Accepted 5 April 2019

1568-9883/© 2019 Published by Elsevier B.V.

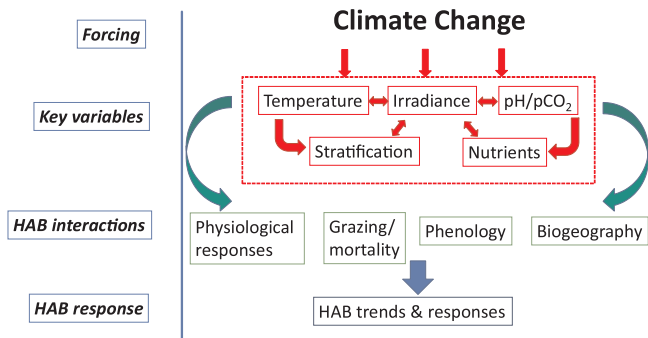


Fig. 1. Climate change related variables and harmful algal bloom (HAB) interactions and resulting responses. Adapted from Wells et al. (2015).

their response to future changes in climate and land use requires an understanding of the physiological and genetic attributes of this group of organisms. New knowledge is needed on the ability of cyanobacteria species to acclimate and adapt to changing conditions, which are likely to vary substantially both temporally and spatially.

Global change effects on ecosystems are varied and interacting, and their effects on cyanobacteria are no different. In a review of harmful algal blooms (HABs) and climate change, Wells et al. (2015) conceptually highlighted the key climate-related variables and their interactions with HABs, and the resulting HAB responses (Fig. 1). The complexity of these interactions makes HAB research related to global changes highly challenging. However, the magnitude of likely problems with cyanobacteria in the future makes this topic highly deserving of scientific attention.

There have been numerous reviews in recent years on the effect of climate change and other globally changing factors, such as eutrophication, on cyanobacteria, e.g. O'Neil et al. (2012); Paerl et al. (2014); Visser et al. (2016); Huisman et al. (2018). In this review, the benefits and challenges of a variety of research approaches for undertaking cyanobacteria research related to global change, across the marine to freshwater continuum, are examined (c.f. Paerl et al., 2018). This review draws together research on both cyanobacteria species attributes (marine, brackish and freshwater), and the effect of physical, biological and nutrient drivers on blooms and dominance of cyanobacteria. Studies that have attempted to reconcile the issues of scale in determining responses are highlighted, as well as the effect of multiple drivers, including climate change, human induced nutrient over-enrichment (eutrophication) and the damming of rivers. Literature for non-cyanobacteria and eukaryotic algae are presented, where there are examples of relevant approaches.

Tackling this global issue will require interdisciplinary research and engagement with the help of interest groups, e.g. the public. Marine and freshwater benthic cyanobacterial mats are included as an example of where research on specific cyanobacterial groups, and their environmental drivers, has been limited and warrants attention (Quiblier et al., 2013; Ford et al., 2018). In addition, climate change effects on cyanobacteria in polar habitats (Antarctica and the Arctic) is still a research gap to be filled.

This review focuses on how best to advance the research agenda, given these challenges. The review provides an up-to-date summary of the pros and cons of different research approaches, including small scale manipulative experiments, contemporary observations, simulation modelling as well as paleolimnological and larger-scale manipulative experiments (Table 1). We advocate for better integration of research across different scales (e.g., from the laboratory to the field) and across different disciplines (e.g., from genetics to environmental policy), to capture the complexity of processes that may affect future scenarios for cyanobacterial bloom development.

Table 1
Summary of research approaches and techniques for the study of global change effects on cyanobacteria.

Techniques	Research Approaches				
	Laboratory cultures	Smaller-scale experimental units in situ	Larger-scale experimental units	Whole-system	Global comparisons
Molecular					
Quantitative PCR	Characterizing genomes of species, strains	Characterizing microbial population (selected genes or genomes)	Characterizing microbial population (selected genes or genomes)	Characterizing microbial population (selected genes or genomes)	Regional and global diversity comparisons
Metabarcoding	Detection or expression of genes linked to physiology	Profiling of specific gene or community-wide gene expression	Profiling of specific gene or community-wide gene expression	Profiling of specific gene or community-wide gene expression	Detection of specific genes
Physiological measures					
Growth indicators	Species and strain responses to global change variables	Population level responses to global change variables	Population level responses to global change variables	Community level responses to global change variables	Diagnostic photophysiology and cellular indicators, e.g. lipids, proteins, carbohydrates
Stress indicators	Controlled competition	Population level responses	Population level responses	Population level responses to global change variables	Identification of long-term community shifts and insights into drivers
Ecology					
Species composition & interactions	Host-parasite interactions	Species competition	Species competition	Species competition	Identification of long-term community shifts and insights into drivers
Environmental variables	Species and strain responses to environmental variables	Predicting physiological responses, validating individual based models, species/strain interactions	Predicting community responses and food-web interactions (e.g., zooplankton grazing)	Predicting community and ecosystem responses using conventional and contemporary (e.g., remote sensing, omics) approaches	Long-term lake simulations of cyanobacteria and eukaryotic communities validated with diagnostic pigments and markers
Modelling					

2. Small scale manipulative experiments to understand species responses

2.1. Laboratory culture studies

Designing experiments of sufficient temporal and spatial scale to provide meaningful predictions of the effect of global changes on cyanobacteria is challenging. Laboratory-scale manipulative experiments are typically used to study the response of individual species to one or more environmental variables. This approach is the backbone of physiological research. Much of the understanding of the physiology of individual species, particularly harmful and nuisance cyanobacteria, has come from laboratory-scale studies, as they allow characterization of responses without the confounding interactions with other species, and avoid the complexities of co-varying environmental conditions (e.g., Fay, 1992; Walsby, 1994; Visser et al., 1997; Sandrini et al., 2014; Schuurmans et al., 2018).

One aspect of global change research where laboratory studies have provided useful insights is the response of cyanobacterial species to temperature. Laboratory studies have identified that cyanobacterial species typically have optimal growth at higher temperatures than dinoflagellates and diatoms, e.g. Paerl et al. (2011); Griffith and Gobler (this issue). Conversely, there were small differences in thermal optima between green algae and cyanobacteria (Lurling et al., 2013). Visser et al. (2016) took these laboratory findings one step further, calculating relative increases in growth rate per unit temperature increase for different species, and showed that the specific growth rates of cyanobacteria tended to increase faster with temperature than those of green algae, although there was considerable variation between species. This is valuable information to help inform predictive models, especially if it can be combined with data on other physiological responses to global change variables, such as enhanced thermal stratification and higher nutrient loadings (Carey et al., 2012).

Lack of uniformity in findings between laboratory studies on the effect of increased CO₂ levels on growth of primary producers prompted a study by Verspagen et al. (2014) to reconcile these differences. They developed a model to test the interplay between pCO₂, light (photosynthetically active radiation, PAR) and nutrient levels on growth, and experimentally tested the model with the cyanobacterium, *Microcystis aeruginosa*. They were able to reconcile contrasting results, demonstrating inorganic carbon limitation at very low pCO₂ levels, whilst nutrient limitation occurred at very low nutrient concentrations, and light limitation in dense phytoplankton blooms at high pCO₂ levels and high nutrient concentrations. This study highlights two key factors: the need to examine multiple drivers of responses, and the need to standardize protocols to ensure reproducibility between laboratory studies.

The effect of global change on competition between phytoplankton species is important for prediction, but has received little attention in the laboratory. This is likely due to the challenging nature of studies which typically require continuous cultures with a high level of regulation and maintenance. Studies of this nature, however, have provided valuable insights, e.g. chemostat experiments of responses of green algae and cyanobacteria to changes in the partial pressure of CO₂ (pCO₂), which were then incorporated into a competition model (Ji et al., 2017). Laboratory studies have also been conducted on *Nodularia spumigena* and *Aphanizomenon* sp., growing together and separately, to determine the combined effect of increased temperature and decreased salinity, and increased temperature and elevated pCO₂ (Karlberg and Wulff, 2013). Outcomes differed in the experiments depending on whether species were grown together or apart, suggesting either allelopathy or resource competition affected dominance. These factors remain poorly understood in the context of global change biology, and are rarely built into predictive models.

2.2. Physiological acclimation and phenotypic plasticity

One of the key challenges in the investigation of the response of cyanobacteria to climate change is that cyanobacterial species are highly flexible in their response. This flexibility can be due to (i) physiological acclimation and phenotypic plasticity (i.e., variation within strains), (ii) genetic variation between strains, and (iii) evolutionary adaptation. This variability complicates the interpretation of laboratory experiments, because results obtained for one set of conditions for one strain in one laboratory may deviate from results obtained with other conditions with other strains in other laboratories. Likewise, this variability also complicates the interpretation of field studies, because cyanobacterial blooms in different lakes or in different years in the same lake may differ in physiological traits, genetic composition and toxin production. This is particularly important if our future climate exceeds present-day windows of climatic variation. The adaptability of cyanobacteria may imply that future cyanobacterial blooms will deviate from present-day blooms not only in terms of frequency, magnitude and duration, but also in terms of their genetic and physiological traits. Despite the challenges imposed by this variability, probably the best way forward is to embrace the aptitude for acclimation and adaptation of cyanobacteria and build it into our research programs.

Controlled laboratory experiments can be very useful in assessing the potential for physiological acclimation and phenotypic plasticity in cyanobacterial strains. One classic field of study is photosynthetic acclimation, and indeed lab experiments have shown major differences in pigmentation, photosynthetic rates and even maximum growth rates between *Microcystis* strains acclimated to low versus high light (Bañares-España et al., 2013). Light color may also have a major effect. In particular, blue light greater than 450 nm is not absorbed by the phycobilisomes of cyanobacteria, and consequently leads to much lower rates of cyanobacterial photosynthesis and growth than light of longer wavelengths (Luimstra et al., 2018).

Toxin production by cyanobacteria is also an important plastic trait. Many cyanotoxins are relatively nitrogen-rich molecules (e.g., microcystins, nodularins, anatoxin-a, saxitoxin), and several laboratory experiments have shown that nitrogen enrichment stimulates production of one of the cyanotoxins, microcystin (e.g., Downing et al., 2005; Van de Waal et al., 2009; Horst et al., 2014). These laboratory results are consistent with multi-year observations from western Lake Erie, where the microcystin contents of *Microcystis* blooms were higher during years with high inorganic nitrogen concentrations than during years of reduced inorganic nitrogen loading (Horst et al., 2014; Gobler et al., 2016).

Temperature is one of the key factors affecting the physiology, morphology and growth of cyanobacteria, as temperature directly affects photosynthesis and cellular metabolism. For instance, laboratory experiments showed that *Raphidiopsis raciborskii* acclimated to high temperature (32 °C) not only grows faster but also develops shorter trichomes in comparison to *R. raciborskii* acclimated to lower temperatures (Soares et al., 2013). These authors report that the same pattern occurred in wild populations of *R. raciborskii* in a tropical reservoir, where shorter trichomes were observed in warmer months. Further work on physiological acclimation of bloom-forming cyanobacteria to rising temperatures and CO₂ concentrations seems highly warranted.

An increasing trend in culture-based studies is the incorporation of -omic techniques, i.e. genomics, transcriptomics and metabolomics (Hennon and Dyhrman, this issue). Transcriptomics has become a valuable method of investigating linkages between genetics, physiology and ecology. Straub et al. (2011) showed that the metabolism of *M. aeruginosa* is compartmentalized between light and dark periods, with greater than 25% of genes varying significantly in their transcript abundance. Harke and Gobler (2015) demonstrated that the global transcriptomic patterns of *M. aeruginosa* changed daily, and varied between nitrogen replete and deficient conditions. During nitrogen

deprivation, genes involved in photosynthesis and respiration, carbon acquisition, lipid metabolism, and amino acid biosynthesis were downregulated, while those linked to nitrogen acquisition and transport were upregulated.

To date, few studies of cyanoHAB species have incorporated metabolomics (the study of the products of metabolism, which are influenced by both genetic and environmental factors; Schwarz et al., 2013). Significant differences in metabolite profiles were observed between toxic and non-toxic strains of *Microcystis* when exposed to varying light conditions, and a comparison between *Microcystis* and the model cyanobacterium *Synechocystis* demonstrated that *Microcystis* invests more in photosynthetic output, i.e. carbon reserves such as glycogen, after high light exposure (Meissner et al., 2015). Steffen et al. (2014) coupled transcriptomic and metabolomics analyses to study *M. aeruginosa* in various nutrient-reduced conditions. Significant gene expression differences were measured between different nutrient treatments. Corresponding metabolomes showed comparably few differences indicating that broad changes to gene transcription are required to maintain metabolic homeostasis. Current and emerging -omic approaches now provide powerful new tools to understand how species utilize their genomic information under different environmental conditions (Mock et al., 2016).

2.3. Genetic variation

It is becoming clear that quantification of the variability in strain (i.e. ecotypes within a species) responses to environmental conditions is a key element of understanding global change-related responses (see review by Lakeman et al., 2009; Raven et al., this issue). Laboratory experiments can play an important role in determining the range of strain responses to environmental conditions. Strains of *Microcystis* and *R. raciborskii* (basinonym *Cylindrospermopsis raciborskii*) were shown to vary in their growth responses to parameters, such as temperature (Xiao et al., 2017a), meaning that predicting how species will compete under different temperature scenarios is complicated. A follow-up modelling study of this data by Xiao et al. (2017b) found that there were no clear winners in terms of dominant strains. A study of 20 *Microcystis* strains also showed wide genetic and phenotypic variation in carbon uptake systems, demonstrating the flexibility of the species to adapt to changing CO₂ conditions (Sandrini et al., 2014, 2015). The authors found variation in gene composition, gene expression and enzymatic activity of the carbon concentrating mechanism between strains.

Microcystis strains also show widely varying responses of aggregation and disaggregation of colonies to turbulence (Li et al., 2018). This has implications for determining their responses under increased global temperatures and climate variability, if it alters the timing and duration of stratification versus turbulent mixing. Studies of strain responses of *R. raciborskii* have also demonstrated intraspecific variation to increased pCO₂ (Pierangelini et al., 2015). The marine cyanobacterium, *Trichodesmium* also showed large strain-specific differences in the relationship between nitrogen fixation and CO₂, suggesting that individual strains within each genus are adapted to grow and fix nitrogen at different CO₂ concentrations (Hutchins et al., 2013). Four strains of the toxic diazotrophic *N. spumigena* also had different intraspecific responses to increased ultraviolet-B radiation (UV-B radiation, 280–320 nm) (Wulff et al., 2007). The significance of these responses also relates to global change as increased greenhouse gas concentrations alter UV-B radiation at the Earth's surface, with potentially different directional changes in UV-B radiation between tropical and polar latitudes (Bais et al., 2011).

Genome comparisons are providing new insights into why different species or strains have varied responses, reinforcing the genetic basis for the strain-to-strain variability described above. Willis et al. (2018) sequenced the genomes of nine *R. raciborskii* strains isolated from a sample from a single lake, and showed an intraspecific variation in

genes associated with environmental responses and adaptation, particularly those involved in phage defence, DNA repair, membrane transport, and stress.

2.4. Evolutionary adaptation

Culture experiments are typically focussed on acclimation, i.e. the degree to which a species has physiological resilience to environmental conditions. This is because most experiments are undertaken with single strains that are assumed to have fixed traits. However, gradual, long term increases in pCO₂ or temperature may also lead to adaptation, i.e. changes in the traits of species driven by natural selection (Hennon and Dyhrman, 2019). Although adaptation is typically a long term change, adaptation to changing environmental conditions may also occur rapidly, on timescales of weeks, through the sorting of existing genetic variation (e.g., Yoshida et al., 2003; Padfield et al., 2015). For example, Sandrini et al. (2016) investigated changes in the strain composition of *Microcystis* in response to rising pCO₂ levels in both laboratory selection experiments and field data. They found that strains containing both high-affinity and high-flux bicarbonate uptake systems prevailed at low pCO₂ levels, but were replaced within a few weeks by strains with only the high-flux bicarbonate uptake system at elevated CO₂. Hutchins et al. (2013) used kinetic constants from the individual CO₂ response curves of strains of both *Trichodesmium* and the unicellular cyanobacterial genus, *Crocospaera*, to show that strains adapted to high pCO₂ concentrations could potentially be favoured in a future acidified ocean.

Some studies have also investigated the implications of natural selection over longer time spans. For example, Hutchins et al. (2015) exposed cultures of the marine bloom-forming cyanobacterium, *Trichodesmium* to a range of pCO₂ concentrations for 4.5 years, then brought them back to contemporary pCO₂ levels. They found that increased growth in response to elevated pCO₂ occurred rapidly, but long-term exposure to higher pCO₂ resulted in permanent changes in fitness of the cultured species to contemporary pCO₂ levels, relative to control cultures. This permanent change in fitness was demonstrated using complementary molecular studies (Walworth et al., 2016). Similarly, Irwin et al. (2015) suggest that some eukaryotic and prokaryotic phytoplankton are adapting to climate change. However, this irreversible response is not consistent amongst studies and species.

Another important consideration is the adaptation of cultures grown long term in the laboratory. Typically, monocultures of cyanobacteria (and eukaryotic algae) are grown in the laboratory under set light and temperature conditions, and exposed to relatively high nutrients concentrations in growth media. This contrasts with field conditions where environmental parameters are constantly changing. There is evidence that these cultures adapt to fixed laboratory conditions, meaning that their traits may gradually deviate from those of natural populations (Lakeman et al., 2009). For example, morphology often changes, and species can lose their toxin producing capacity. Overall, the research outlined above highlights that laboratory experiments need to be carefully designed, taking into account adaptation and acclimation responses of individual species and strains.

2.5. The issue of scale

Another challenge with laboratory experiments is understanding the relevance of scientific findings to global scale predictions. One reason for this is that laboratory studies cannot readily examine responses to physical factors, such as stratification and turbulence, which affect cyanobacterial blooms across larger spatial scales than the typical Erlenmeyer or culture flask, and hence cannot be easily studied at the laboratory scale. This highlights a key dilemma in undertaking laboratory experiments: Are culture conditions appropriate for predicting real world responses? Are there other approaches that would be more helpful to enable better predictive capability?

2.6. Small-scale in situ experimental units

Small-scale manipulative experiments in the field provide another approach to understanding responses of cyanoHABs species to global change. The advantage of these studies over laboratory studies is that species have not acclimated to laboratory conditions, and species interactions are implicitly embedded within the experiment (Lakeman et al., 2009). Compared to laboratory studies, relatively few microcosm experiments have been conducted. A study of the response of *Trichodesmium* colonies to a range of pCO₂ levels in field studies showed no enhancement of nitrogen or carbon fixation in response to changes in pCO₂ levels (Gradoville et al., 2014). The authors concluded that the lack of response was due to the interacting effects of strains and other nitrogen fixers within the colonies. In outdoor experiments, Davis et al. (2009) showed that higher temperatures coupled with elevated phosphorus concentrations frequently yielded higher growth rates of toxic *Microcystis* cells over non-toxic cells.

The effect of UV radiation (280–400 nm wavelength), nutrients, pCO₂ and salinity on diazotrophic filamentous cyanobacteria and associated natural microplanktonic communities in the Baltic Sea was examined with outdoor factorial experiments. Studies showed that filamentous cyanobacteria tolerated relatively high ambient radiation conditions, including ultraviolet radiation, even when they were nutrient limited (Mohlin and Wulff, 2009; Pattanaik et al., 2010; Mohlin et al., 2012). Cyanobacteria were not negatively affected by increased pCO₂ (Wulff et al., 2018; Olofsson et al., in press) but decreased salinity had a species-specific effect (Wulff et al., 2018). This highlights the importance of considering multiple stressors as well as multiple species Griffith and Gobler (this issue).

3. Larger-scale experimental units

Larger-scale experimental units (sometimes called mesocosms) provide another useful intermediary step between laboratory studies and lake-scale studies. They involve larger-scale vessels than smaller scale experimental units (typically many litres). They also have the benefit of more realistic conditions than the laboratory, as well as the ability to test the effect of a range of drivers individually, or in combination. They are expensive and logistically challenging to undertake, so relatively few studies have been conducted. Hansson et al. (2013), for example, undertook a study with larger-scale experimental units to show that higher humic levels in water, combined with higher temperature, promoted higher growth rates of the cyanobacterium, *Microcystis*, compared with temperature alone.

An enclosed experimental study of coastal rocky shores showed that the combination of ocean acidification (elevated pCO₂) and global warming promoted benthic cyanobacteria over other species (Ullah et al., 2018). These authors also found that cyanobacteria did not fuel productivity of higher trophic levels, but rather promoted a detrital-driven food web, possibly because cyanobacteria can be a poor quality food source. Another study in larger-scale experimental units (55 m³) in the Gulf of Finland found that the biomass of cyanobacteria cells > 5 µm diameter was not significantly affected by elevated pCO₂ (Bermúdez et al., 2016; Paul et al., 2016), but the biomass of the picocyanobacterium, *Synechococcus* was negatively affected (Crawford et al., 2017).

Larger-scale experimental units have a range of benefits in promoting understanding of the responses of cyanobacteria to global change, but they also have limitations, such as the timing of the experimental period, dealing with top down factors in an effective way, e.g. grazing, wall effects, and over time, dramatic deviations from the 'real world' if experiments are run for too long. Moreover, it is challenging to manipulate cyanobacterial densities and nutrient concentrations simultaneously in larger-scale experimental units, hindering our understanding of cyanobacterial responses to different interacting global change stressors. To create experimental cyanoHABs in these

units, some researchers add cyanobacteria in nutrient-rich culture media or have added nutrients to stimulate cyanobacterial growth, thereby conflating the effects of the cyanobacteria and nutrients (e.g., Rondel et al., 2008). For some large colonial cyanobacteria, it is possible to manipulate colonies individually to disentangle the effects of cyanobacteria on nutrient cycling (e.g., Engström-Öst et al., 2013; Carey et al., 2014), but this approach is not possible for smaller taxa and picocyanobacteria.

4. Ecosystem scale observations

Whole-system observations have played an important role in understanding how global changes, such as global warming, are affecting seasonal patterns. For example, in higher latitude regions, lakes and reservoirs have experienced earlier "ice off" and later "ice on" times during the year, thereby expanding the "window of opportunity" for blooms to form and persist (Stüken et al., 2006; Peeters et al., 2007; Suikkanen et al., 2007). Earlier warming of surface waters can also lead to a more rapid onset of vertical-density stratification, known to favour buoyant surface-dwelling cyanoHABs (Jöhnk et al., 2008; Paerl and Huisman, 2008, 2009). The time of year that warming occurs can also be critical (Winder and Sommer, 2012), with studies in large peri-alpine lakes showing that cyanobacteria did not increase in abundance in warmer summers, but rather in warmer autumn and winter periods (Anneville et al., 2015). In some cases, lakes and reservoirs previously exhibiting winter ice cover are now ice-free. These changes have greatly altered the regional scales and magnitude of cyanoHABs (Wiedner et al., 2007; Wagner and Adrian, 2009).

The relative role of multiple drivers of cyanoHABs is more difficult to differentiate in ecosystem-scale studies (Glibert, this issue). However, in an analysis of ~1000 lakes across the U.S., Rigosi et al. (2015) found that nutrients were a more important driver of cyanoHABs than temperature, but that the importance of the relative effects varied with cyanobacterial taxon and lake trophic state. Complementing Rigosi's et al. (2015) study, a study of 143 lakes along a latitudinal gradient in South America showed an interplay between temperature, light and nutrients (Kosten et al., 2012). They found that the proportion of cyanobacteria, relative to other phytoplankton groups, rose steeply with increased temperature, but lakes with high rates of light absorption also have a higher percentage of cyanobacteria. Light limitation is often driven by high algal biomass, which, in turn, is often driven by high nutrient levels. These effects can feed back to increased water temperature and enhance stratification, reinforcing the dominance of cyanobacteria (Kumagai et al., 2000). In some studies, the type of seasonal lake mixing regime (polymictic vs monomictic) may even be regulated by the biomass of phytoplankton (Shatwell et al., 2016).

Another symptom of a changing climate is increasing variability and more extreme precipitation events. Storm events, including tropical cyclones, seasonal windy periods, and summer thunderstorms, are regionally becoming more extreme, and have higher amounts and intensities of rainfall (Webster et al., 2005; IPCC, 2007, 2012; Allan and Soden, 2008; Bender et al., 2010). Conversely, droughts are becoming more severe and protracted (Trenberth, 2005). These events cause large changes in hydrologic variability, i.e., wetter wet periods and drier dry periods. This has led to more episodic discharge periods in which large amounts of nutrients are captured and transported in runoff events causing nutrient enrichment of receiving waters. If such events are followed by periods of extended drought in which freshwater flow decreases dramatically and residence time of receiving waters increases, conditions are more likely to favour cyanoHABs (Paerl et al., 2011). This is particularly evident if storms are accompanied by warming, since cyanobacteria typically have relatively slow growth rates compared with eukaryotic algae at moderate temperatures (Butterwick et al., 2005), but relatively higher growth rates in a warmer climate (Paul, 2008; Paerl and Paul, 2012; Lehman et al., 2017). Another important positive effect of storms on cyanoHABs is increasing mixing at

the sediment-water interface, which can both mobilize nutrients as well as stimulate the recruitment of cyanobacteria with dormant resting stages (e.g., benthic cells, akinetes) (Karlsson-Elfgren et al., 2004; Carey et al., 2014).

Strong interannual climate variability has major impacts on the succession of phytoplankton species, as demonstrated by Wood et al. (2017a) in a shallow lake where cyanoHAB species proliferated. These authors found that *Microcystis* blooms occurred when ammonium concentrations and water temperature increased in a wet summer, whereas nitrogen-fixing genera (*Dolichospermum*, *Chrysosporum*) dominated in the following dry summer when there were low concentrations of dissolved inorganic nitrogen. The implications of this study are that changes in the timing and duration of droughts and runoff events from climate change are likely to affect the succession of cyanoHAB species.

A valuable new tool for teasing apart species level responses and gaining insights into community-wide physiological adaptation in field studies is meta-transcriptomics; the sequencing of transcripts directly from environmental RNA. In Lake Erie (Ohio, USA) this approach has been coupled with field surveys, and experiments to provide new knowledge on niche requirements of the three key bloom forming taxa (*Microcystis*, *Planktothrix*, and *Dolichospermum*; Steffen et al., 2015; Harke et al., 2016). Their data demonstrate the utilization of different nutrient acquisition mechanisms among taxa (e.g. nitrogen fixation, phosphorus scavenging) and defence strategies (e.g., viral defence, protease inhibitors) that results in partitioning in the abundance of the taxa across the western basin of the lake. Meta-transcriptomic studies in the Baltic Sea, northern Europe and Lake Taihu (China), highlight the integral and important role that associated heterotrophic bacteria play in regulating cyanobacterial blooms (Teikari et al., 2018; Chen et al., 2018).

5. Looking back to predict the future

Understanding whether lakes have always experienced cyanobacterial blooms, and if recently reported bloom-forming species have always been present but are now responding to environmental change, is hampered by a lack of long-term datasets. Increasing knowledge on the composition of cyanobacterial communities over long periods may enable mechanisms of ecological change to be determined, and assist in predicting future responses. Paleolimnology provides a useful approach to study historic shifts in biological structure and functioning. The use of environmental DNA (eDNA) in concert with recently developed molecular tools now provides a means of identifying soft-bodied organisms (Domaizon et al., 2017).

Recent paleolimnological studies incorporating eDNA techniques, and in some case pigments (zeaxanthin and echinenone are commonly used for cyanobacteria), have provided new knowledge on how and why cyanobacterial abundance and diversity is changing, e.g. Bianchi et al. (2000). Pal et al. (2015) combined pigment and quantitative PCR (targeting cyanobacterial specific 16S rRNA genes) analysis of cores collected from five lakes in western Quebec (Canada). They found that cyanobacterial abundances increased over the past 30 years in lakes located in both protected conservation land and non-protected areas with no significant differences between them. Based on this observation, the authors argue that factors other than land use change, such as a warming climate, are likely responsible. A recent large-scale collation of data from northern temperate subarctic lakes, based on sedimentary pigments, revealed that cyanobacterial abundance has increased over the past 200 years relative to other phytoplankton taxa (Taranu et al., 2015). In contrast to the study of Pal et al. (2015), the authors suggest nutrient concentrations were the primary driver of cyanobacteria increases, with temperature changes having a secondary influence.

Monchamp et al. (2016) used high-throughput sequencing to explore cyanobacterial community structure over the last 200 years in two perialpine lakes (Greifensee and Zurich, Switzerland). Changes in

diversity were observed, and the microcystin synthetase gene *mcyA* was amplified, confirming the presence of potentially toxic cyanobacterial taxa over recent years in Greifensee and throughout the last century in Lake Zurich. Sedimentary DNA has also been used to investigate: the past distribution of potentially toxic *Microcystis* in Lake Erie USA, (Rinta-Kanto et al., 2009); the presence of the saxitoxin-producing *R. raciborskii* and *sxtU* gene (involved in saxitoxin biosynthesis) in a subtropical lagoon in Uruguay (Martínez et al., 2017); and cyanobacterial communities shifts, including the presence of anatoxin-producing *Cuspidothrix issatschenkoi*, over the last 150 years in a temperate lake in New Zealand (Wood et al., 2008).

Zastepa et al. (2017) worked on Baptiste Lake (Alberta, Canada) and detected microcystins in sediments pre-dating any significant alteration to the watershed, demonstrating that the presence of toxic cyanobacteria may not be a recent phenomenon in eutrophic ecosystems. After 2000, concentrations of microcystins increased and were strongly correlated with increases in nitrogen and phosphorus concentrations, while there was no relationship with climate-related variables. Applying eDNA, pigment and cyanotoxin analysis to sediment cores collected from a wide array of lakes globally, where both natural, anthropogenic and climatic stressors vary, has the potential to greatly enhance knowledge on the long-term drivers of cyanobacteria and toxin shifts, and assist in predicting future change.

Beyond studies in sediments, there are limited long-term studies of changes in cyanoHAB abundance, however they can provide strong evidence for global changes in bloom drivers. The brackish Baltic Sea is an example of an ecosystem that has been exposed to elevated levels of nutrient loading for decades, and it is difficult to separate these effects from climate change effects on the dominant cyanoHAB species, *N. spumigena*. However, in a compilation of a 35-year time series, Kahru and Elmgren (2014) observed that the biomass accumulation period occurred progressively earlier by ca. 0.6 days yearly (20 days over 35 years). The reasons could be several, however the period of the year with sea surface temperatures of 17 °C or more has almost doubled from 1982 (29 days 1982, 56 days 2014; Kahru et al., 2016).

6. Gaps in knowledge - benthic cyanoHABs

Much of the focus on cyanoHABs has been on pelagic species which impact drinking water supplies, e.g. *Microcystis*, *Dolichospermum*, *Raphiopsis*. However, toxic benthic cyanoHABs appear to be increasing, although they have received less attention. Under certain environmental conditions these benthic cyanobacterial mats can proliferate and cover extended areas of the substrate in streams, lakes and marine environments (Scott and Marcarelli, 2012; Villeneuve et al., 2012). While these mats occur naturally, they are increasingly prevalent in a range of habitats, including wadeable rivers (Fetscher et al., 2015; McAllister et al., 2016; Bouma-Gregson et al., 2018), lakes, especially in littoral zones (Smith et al., 2012; Belykh et al., 2017), and coastal lagoons (Stal et al., 1996; Méjean et al., 2010). The effects of climatic change, such as warmer water temperatures and longer drought periods, are predicted to favour the proliferation of benthic species in many habitats (Quiblier et al., 2013; Echenique-Subiabre et al., 2015). This includes polar regions where both increased temperature and glacier meltwater ponds/streams provide an increasingly occurring, creating favourable habitat for benthic cyanobacteria (Zakhia et al., 2008). This has been observed on King George Island, Antarctica (Komarek and Komarek, 2001). An increasing number of the taxa in these mats are now known to produce cyanotoxins. Ingestion of toxic mats has been associated with animal deaths, and there have been numerous human health warnings (Quiblier et al., 2013; McAllister et al., 2016).

Ideally, studies of cyanoHABs should focus across scales, from the molecule to the ecosystem. An example of bridging these scales has been used to investigate drivers of growth of anatoxin-producing *Microcoleus* (previously *Phormidium*) blooms in wadeable streams in

New Zealand. This has included molecular studies examining microbial communities (Brasell et al., 2015), and abundances of genotypes (Wood and Puddick, 2017), combined with culture-based laboratory studies (Heath et al., 2016), field studies spanning a range of temporal and spatial scales (Wood et al., 2017b; McAllister et al., 2018a), and manipulative larger-scale experimental studies (McAllister et al., 2018b).

Laboratory studies that encompass a greater diversity of species, field studies that span longer time periods and greater spatial scales, and larger-scale experimental studies are needed to address the shortfall of information on benthic cyanobacteria. Experimental work needs to be carefully planned to ensure that there are realistic simulations of the interactions between cyanobacteria and their substrate (i.e. bottom sediments from which nutrients are sourced), with the water column interface, and with co-occurring prokaryotic and eukaryotic organisms involved in succession and nutrient cycling (Bolhuis et al., 2013).

Further studies investigating the causes of benthic cyanobacterial proliferations may ultimately lead to the development of models that can be used to predict times of greatest risk, and also be used to streamline monitoring regimes. For example, simple models based on stream flow and time of year show promise for estimating benthic cyanobacteria cover in real-time at specific sites in rivers in New Zealand (e.g., Thomson-Laing et al., 2018).

7. Predictions

As Niels Bohr once noted, “prediction is difficult, especially about the future”. This may particularly apply to ecological studies of cyanobacteria with their high levels of phenotypic plasticity and genetic diversity. However, studies of population dynamics of cyanobacteria using reductionist approaches in the laboratory and in microcosms, have been useful for studying environmental influences on cyanobacteria dynamics. The species traits measured in these studies can be implemented in process-based mechanistic models, and the model predictions can subsequently be tested using controlled monoculture and competition experiments. There are many examples where models have been very successful in predicting phytoplankton growth under nutrient-limited conditions (Droop, 1973, 1974; Klausmeier et al., 2004), and these models have provided the cornerstone for resource competition theory (Tilman, 1982; Grover, 1997; Burson et al., 2018). Models and experiments have since been extended to predict cyanobacterial growth and competition under light-limited conditions, first treating light as single resource (Huisman and Weissing, 1994; Huisman et al., 1999; Litchman and Klausmeier, 2001; Passarge et al., 2006), and later taking the full light spectrum into account (Stomp et al., 2004, 2007, 2008). Furthermore, nitrogen fixation has been included (Agawin et al., 2007; Hellweger et al., 2016) as well as carbon-limited conditions, to account for predicted effects of rising CO₂ concentrations (Van de Waal et al., 2011; Verspagen et al., 2014; Ji et al., 2017).

The results of these process-based studies provide a sound basis for implementation of the mathematical models as modules in larger ecosystem simulation models of cyanobacterial blooms, such as PC-Lake (Janse, 1997; Janssen et al., 2019), DYRESM-CAEDYM (Trolle et al., 2012; Hamilton et al., 2014b), PROTECH (Reynolds et al., 2001; Elliott, 2010) and SCOB (Eilola et al., 2009; Hieronymus et al., 2018). For nutrient and light limitation this has already been done, but most ecosystem models do not yet include the full underwater light spectrum or inorganic carbon chemistry, and in the upcoming years, advances need to be made in these areas (Hipsey et al., 2015).

Although accurate prediction under controlled laboratory conditions is feasible, it is much more difficult to accurately predict the development of cyanobacterial blooms in lakes. Harris (1994) espoused a goal that models should be able to produce “predictions of the species composition of the phytoplankton community including the possibility of toxicity”. Yet this goal has remained elusive for three main reasons. First, although laboratory experiments typically use the simplifying assumption that the cyanobacterial population is homogeneously

mixed, in reality, cyanobacteria in lakes are not uniformly distributed in the water column or benthos (Puddick et al., 2016). They are transported by a variety of processes at different spatial and temporal scales, including directional flows generated by currents, the more random motion generated by turbulence, and the directed movement of cyanobacteria by sinking and buoyancy of the cells and colonies (Ndong et al., 2017). These transport processes need to be considered, for instance to predict the accumulation of a *Microcystis* population as a surface bloom at the leeward side of a lake (Huisman et al., 2004; Hunter et al., 2008), or metalimnetic accumulations of *Planktothrix* (Carraro et al., 2014).

Secondly, cyanobacteria are embedded in food webs in multiple ways, as food for other organisms, as hosts for viruses and parasites, or through the “microbial loop” (DeMott et al., 1991; Haraldsson et al., 2018; Huisman et al., 2018). Hence, their proliferation can be affected by a multitude of other species. Interactions between multiple species at multiple trophic levels within the food web can lead to alternative stable states in species composition, and complex nonlinear dynamics. For instance, interactions with zooplankton and viruses can lead to a dramatic collapse of a cyanobacterial population that can be succeeded by the re-invasion of new species that are less edible or more resistant to viral infection (Yoshida et al., 2008; Lemaire et al., 2012; Gerphagnon et al., 2017). These highly dynamic phenomena create limits on the forecast horizon for accurate predictions of the species abundances in plankton communities (Benincà et al., 2008; Petchey et al., 2015). Over short time scales, some of these effects can be modelled, including how the virus-cyanobacteria host interactions may theoretically result in population collapses, and interactions with phosphorus and light-limited growth (Gons et al., 2006). Theoretical predictions repeatedly emphasize, however, that cyanobacteria–phage interactions rapidly alter biogeochemical cycles through processes such as cell lysis, which propagate through to succession in the planktonic community composition (Cairns et al., 2016). Similar rapid transformations have been demonstrated in a larger-scale experimental study with a planktonic food web isolated from the Baltic Sea, where the species abundances fluctuated strongly over several orders of magnitude for more than six years. It was estimated that the population dynamics of these species were only predictable for up to about 15–30 days in advance (Benincà et al., 2008).

Thirdly, natural ecosystems are exposed to variable environmental conditions, which include both deterministic components, e.g. seasonal cycle, and more stochastic weather events, e.g. day-to-day variability and episodic events. The weather itself has a forecast horizon for successful prediction of only about two weeks or so. Yet, the weather may have a tremendous impact on cyanobacterial bloom development. For instance, a prolonged warm period with little wind action will have a very different effect on cyanobacterial blooms than a short summer heatwave that ends in thunderstorms (cf., Paerl et al., 2016). Similarly, droughts and floods drive different cyanobacteria assemblages (see Section 3.2). Again, this makes it difficult to forecast cyanobacteria far in advance. Like the weather forecast, suitable early-warning systems for Cyanobacteria will therefore require intensive monitoring of the plankton community, nutrients and weather conditions at a sufficient spatial and temporal resolution to update the model forecasts on a regular basis, by means of data assimilation techniques (Dietze, 2017; Massoud et al., 2018).

Data assimilation has found widespread application and use in many fields of research, including hydrology, oceanography and satellite remote sensing (e.g., Lawson et al., 1996; Vrugt et al., 2005; Seppala et al., 2007; Xiao and Friedrichs, 2014; Gehlen et al., 2015). In particular, remote sensing studies, coupled with on-site monitoring stations using a combination of traditional and modern measurements (e.g., toxin genes, Bukowska et al., 2017; or phycocyanin sensors, Bertone et al., 2018), may provide excellent tools to validate early-warning systems for ecologically and economically important lakes. This field is evolving rapidly with the recent advent of operational

satellites (e.g. Envisat with MERIS sensor, Sentinel-3 (A and B) with OLCI sensor) that have sensor detection wavebands aligned with the phycocyanin absorption waveband around 625 nm. In other cases, airborne hyperspectral sensor measurements may even allow cyanobacteria to be distinguished at a genus level (*Chrysosporum*, *Microcystis*) (Kudela et al., 2015). These approaches can interface with a variety of predictive modelling methods, including data-driven techniques of physically based numerical simulation (Lake Geneva, France/Switzerland, Soullignac et al., 2018), or statistical tools using artificial neural networks or evolutionary computational methods (Lake Kinneret, Israel, Recknagel et al., 2014; Lake Taihu, China, Zhang et al., 2015), to provide high temporal and spatial resolution data suitable for validate and improve these models.

Looking ahead, even if we cannot predict the actual weather for any specific date beyond a two-week forecast horizon, we can predict the expected average climate for the years 2040–2100. Likewise, we can still predict the average probability of occurrence of cyanobacterial blooms. A rich literature now exists documenting predictions from numerical and statistical models of more intense and prolonged cyanohAB events in a future warmer climate (e.g., Howard and Easthope, 2002; Elliott, 2012; Trolle et al., 2011; Rigosi et al., 2015; Moe et al., 2016). For instance, an advanced cyanobacterial life cycle model was combined with a coupled biological-physical model and the projections of a regional climate model to predict cyanobacterial abundances in the Baltic Sea (Hense et al., 2013). The model predicts that the 30-year average of cyanobacterial biomass and nitrogen fixation will increase more than twofold from the years 1969–1998 to the years 2069–2098. Furthermore, a recent study used climate change projections from five global circulation models as input for a coupled water quantity and quality model of USA lakes (Chapra et al., 2017). This model predicts that the mean number of days with harmful cyanobacterial blooms in the USA will increase from about 7 days per year per waterbody under current conditions to 18–39 days in 2090. However, nearly all of the above-mentioned models have deficiencies, pointing to where future work is needed.

One deficiency in cyanohAB models is that many well-known physiological attributes of cyanohAB species (see reviews by Carey et al., 2012; O'Neil et al., 2012; Oliver et al., 2012) are likely to be differentially impacted by interacting changes in temperature and stratification. These interactions are not included in many of the ecosystem models used to predict cyanohABs in a changing climate. While much progress has been made with individual-based models of nitrogen fixation (Hellweger et al., 2008), buoyancy regulation (Wallace et al., 2000), and aggregation and disaggregation of colonial *Microcystis* at different levels of turbulence (Ndong et al., 2017; Li et al., 2018), these sub-models are generally not included in lake ecosystem models applied to examine climate change impacts on cyanohABs. As a result, we lack the species-level numerical predictions that could be used to test our theories of the dominant cyanohAB species and successional sequences we might expect with a changing climate (Dokulil and Teubner, 2000; Carey et al., 2012).

A second limitation to our ability to predict climate change impacts on cyanohABs, is a lack of integration with catchment models, as changes in discharge and contaminant loads may potentially have synergistic or antagonistic interactions with internal lake processes (Hamilton et al., 2016). Recent exceptions include integrated coupled climate-catchment-lake models (Soullignac et al., 2018), some of which have been used to examine climate change impacts at the lake ecosystem scale (Me et al., 2018).

In summary, we will need process-based studies to further unravel the myriad of physiological and ecological processes that may affect cyanobacterial bloom dynamics, and incorporate the insights from these process-based studies in larger ecosystem models. Furthermore, we will need to embrace data assimilation techniques to fuse inputs from high-resolution monitoring stations into ecosystem models, with the aim to advance early-warning systems for the short-term prediction

of cyanobacterial blooms over time spans of weeks. Last, but not least, we will need linkages between climate models, socio-economic scenarios and ecosystem models to predict expected long-term changes in cyanohABs phenology under different scenarios of global change.

8. Global multi-system initiatives

Given the severity of increasing cyanohABs in many regions globally, it is critical that an “all hands on deck” approach is used to address this problem. In particular, we advocate for increased collaboration among different research disciplines, stakeholder groups, managers, and policy- and decision-makers to advance cyanobacterial research, management and long-term control. CyanohABs provide an ideal catalyst for collaboration between theoretical and applied researchers across many different fields. For example, the knowledge that molecular biologists, physiologists, and biochemists gain from studying cyanobacteria in the laboratory is needed to interpret the information collected by ecologists in the field and vice versa. Similarly, the need for modelers to simulate the effects of potential treatment measures (e.g., Huisman et al., 2018) can provide critical information for guiding implementation by managers on the ground, thereby also driving the research agenda for modelers.

In addition to engineering and the natural sciences, researchers from the social sciences, political science, and economics provide valuable perspectives needed to understand and manage blooms within a coupled natural-human system (Van Dolah et al., 2016; Cobourn et al., 2018). For example, studying the physiology and ecology of bloom-forming taxa can guide how utilities and managers should best extract water for drinking. In turn, studying policy interventions and economic incentives for catchment (= watershed) remediation to decrease cyanohAB blooms can help prioritize field monitoring and management efforts.

In addition to integration of the workforce of cyanohAB researchers working across disciplines, changing the way cyanobacterial research is conducted will also advance the field. The development of grassroots efforts to collect and share data has already improved understanding of cyanobacterial dynamics across many freshwater ecosystems. Two notable examples are the Global Lake Ecological Observatory Network (GLEON) and the European Multi-Lake Survey (EMLS). GLEON is a grassroots organization of ecologists, engineers, computer scientists and limnologists working together to advance understanding of how lakes respond to human activities and global change by deploying sensorized platforms in waterbodies around the world (Weathers et al., 2013; Hamilton et al., 2014b). GLEON researchers are synthesizing datasets to study the vertical distribution of cyanobacteria and other phytoplankton (Brentrup et al., 2016), identify the drivers of sub-surface blooms (Leach et al., 2018), and use sensor data to drive phytoplankton bloom models (e.g., Hamilton et al., 2014b; Page et al., 2017).

Similarly, the EMLS is a collaborative effort by researchers in 26 European countries to sample 369 lakes to determine the drivers of cyanobacterial bloom formation across Europe (Mantzouki et al., 2018; Mantzouki and Ibelings, 2018). To date, data from the EMLS suggest that temperature is the main driver of the spatial distribution in cyanobacterial toxins across Europe. These grassroots efforts complement ongoing centralized monitoring led by federal agencies and other research programs.

Researchers are also trying to bridge the divide between the study of eukaryotic HABs and cyanohABs in marine, brackish and freshwater, and between researchers and policymakers, with the global initiative, GlobalHAB (www.globalhab.info/). This program is promoting international research, observations and modelling of harmful algal blooms in aquatic systems by sharing information globally via workshops, conferences and other communication means (GlobalHAB, 2017).

The proliferation of community-based science integrating data collected by many researchers, as well as citizen scientists, has much to promise for improving understanding of cyanobacterial blooms.

Tapping into citizen scientist datasets, collected via mobile phone apps, such as LakeObserver (lakeobserver.org), provides the opportunity to collect cyanobacterial data on temporal and spatial scales previously impossible for traditional research programs. Integrating these diverse datasets into models using data-fusion approaches, such as those now increasingly used by the terrestrial research community (e.g., LeBauer et al., 2013; Thomas et al., 2017) will provide new information on the distribution and ecology of blooms. This is critical to our ability to predict and manage blooms into the future, as they continue to have social, environmental and economic impacts.

9. Summary

Small and large scale experiments and observations to examine responses of cyanoHABs to globally changing environmental parameters all have a key role to play in research on global change and cyanoHABs, depending on the specific research question/s or hypotheses being tested (Table 1). Additionally, all approaches have limitations, and it is likely that the greatest insights will come from a combination of approaches, techniques, species/strains and testing of environmental factors across the freshwater to marine continuum. Such integration should be combined with: increased sharing of data by interdisciplinary (e.g., from genetics to environmental policy), cross-system, (i.e. watershed to receiving waters), international teams of researchers; the development of new mechanisms for collaboration; and the integration of diverse datasets across different scales (e.g., from the laboratory to the field), to advance the research agenda for improving understanding of cyanoHABs in a future of global change.

Acknowledgements

The following authors were supported as follows: M.A. Burford from Australian Research Council Linkage grant LP120100284, C.C. Carey from the U.S. National Science Foundation (EF-1702506, CNS-1737424, ICER-1517823), H.W. Paerl from USA National Science Foundation CBET0826819 and Dimensions in Biodiversity1831096, S.A. Wood and D.P. Hamilton from the New Zealand Ministry of Business, Innovation and Employment (UOWX1503; Enhancing the health and resilience of New Zealand lakes, and C05 × 1707; Our lakes health; past, present and future), A. Wulff from the Carl Trygger Foundation and the Union FP7 Project IMCONet (Grant agreement No 319718). References compiled by S. Faggetter.[CG]

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